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## Contextual effects on decision templates for parafoveal orientation identification

Isabelle Mareschal\*, Michael J. Morgan, Joshua A. Solomon

Department of Optometry and Visual Science, City University, London EC1V 0HB, UK

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### ABSTRACT

When a peripherally viewed stimulus is presented with flankers, observers' acuity for shape generally decreases. We wondered whether a change in the locus of information accrual accompanied these performance deficits and employed psychophysical reverse correlation to find out. Surrounding the target (a near-vertical Gabor patch) with a vertical grating caused a slight elongation and a rotation in the decision templates for orientation identification. We also found that the contrast required to maintain criterion performance in this condition was actually lower than it was in a target-alone condition. However, this facilitation decreased with practice, due to perceptual learning in the target-alone condition. Unlike a continuous surround, isolated flanks elevated contrast thresholds, but decision templates were similar with both of these contexts. The rotation of decision templates (off-orientation looking) suggests that performance is limited by additive internal noise. We speculate that this noise can be reduced when the target is easily segregated from its surround.

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### 1. Introduction

Observers are able to make very fine orientation discriminations even though orientation tuned channels have broad bandwidths. Regan and Beverley (1985) proposed that orientation discrimination does not rely on the output of the most active channel, but rather on the relative response of a group of channels to a given stimulus. By monitoring relative activities, orientation can be accurately encoded without being confounded with signal strength (i.e. contrast).

For stimuli presented outside the fovea, it has been found that the discrimination of orientation is usually hindered by the presence of nearby stimuli. This effect of visual context is known as crowding (e.g. Bouma, 1970; Chung, Levi, & Legge, 2001; Levi, Klein, & Hariharan, 2002; Loomis, 1978; Parkes, Lund, Angelucci, Solomon, & Morgan 2001; Pelli, Palomares, & Majaj, 2004; Wilkinson, Wilson, & Ellember, 1997). Crowding can be distinguished from contrast masking because (i) the effects of flankers are spatially anisotropic (Feng, Jiang, & He, 2007; Livne & Sagi, 2007; Petrov, Popple, & Mc Kee, 2007), (ii) effects increase with eccentricity, but remain independent of stimulus size (Chung et al., 2001; Levi et al., 2002), and (iii) unlike masking, crowding leaves detection relatively unimpaired (Pelli et al. 2004).

There are many accounts for crowding, but the most common explanation is that it reflects an inappropriate combination of fea-

tures from the target and the flankers, occurring at a second stage of image processing, the "integrator" unit (i.e. Levi et al., 2002; Parkes et al. 2001; Pelli et al. 2004). An alternative account of crowding is that it results from the limited spatial resolution of attention (He, Cavanaugh, & Intriligator 1996; Strasburger, 2005; Tripathy & Cavanaugh, 2002). It is worth noting that these two accounts are not mutually exclusive.

An increasingly popular way to characterize visual selectivity is to correlate the behaviour of a sensory system with some stochastically varying stimulus attribute (typically the luminance of pixels in white noise). This technique has been used both in physiology to derive a neuron's receptive fields (DeAngelis, Ohzawa, & Freeman 1993; Emerson, Bergen, & Adelson 1992; Ohzawa, DeAngelis, & Freeman 1997; Ringach, Hawken, & Shapley 1997) and in psychophysics to determine an observer's "perceptive field" or decision template, i.e. the region in space that determines performance (e.g. Abbey & Eckstein, 2002; Ahumada, 2002; Dakin & Bex, 2003; Gold, Murray, Bennett, & Sekuler, 2000; Levi & Klein, 2002; Mareschal, Dakin, & Bex 2006; Murray, Bennet, & Sekuler 2002; Nandy & Tjan, 2007; Neri & Heeger, 2002; Solomon, 2002). In psychophysics, unbiased estimates of the decision template can be derived using the classification-image analysis (Ahumada, 1996; Abbey, Eckstein, & Bochud, 1999).

Here we employ classification-image analysis to determine how the decision template for parafoveal orientation discrimination is affected by visual context. In particular, we examined classification-images to see whether they included the nearby stimuli, as would be expected from the feature-combination account of crowding. Our most surprising result was that some very salient visual contexts, which completely surrounded the target, actually

\* Corresponding author.

E-mail addresses: [Isabelle.Mareschal.1@city.ac.uk](mailto:Isabelle.Mareschal.1@city.ac.uk), [imareschal@gmail.com](mailto:imareschal@gmail.com) (I. Mareschal), [m.j.morgan@city.ac.uk](mailto:m.j.morgan@city.ac.uk) (M.J. Morgan), [J.A.solomon@city.ac.uk](mailto:J.A.solomon@city.ac.uk) (J.A. Solomon).

helped, rather than hindered parafoveal orientation discrimination by lowering observers' decision noise.

## 2. Methods

### 2.1. Observers

Two of the authors (I.M. and J.A.S.) and one naive subject (A.T.) served as observers. All wore optical correction as necessary.

### 2.2. Apparatus and stimuli

An Apple Macintosh G4 computer running MATLAB™ (MathWorks Ltd.) was used for stimulus generation, experiment control and recording subjects' responses. The programs controlling the experiment incorporated elements of the PsychToolbox. Stimuli were displayed on a ValueVision monitor (1280 × 1024 pixel, frame refresh rate 60 Hz) driven by the computer's built-in graphics card. We achieved true 14-bit contrast resolution in grey-scale using a Bits++ system (Cambridge Research Systems). The display was calibrated using a photometer and linearised using look-up tables in software.

#### 2.2.1. Target and noise

In the target-alone condition (Fig. 1a), the stimulus was a  $96 \times 96$  pixel white noise image presented either  $5^\circ$  to the left or right of fixation for 150 ms. At the viewing distance, one pixel subtended 2.1 arcmin. The luminance of each pixel was uniformly distributed over either one-fourth (observers I.M. and A.T.) or one-half (J.A.S.) the available range of intensities. In its center was a Gabor patch, the product of a sinusoidal carrier (2.37 c/deg) and a circular Gaussian window (with spread  $\sigma = 0.21^\circ$ ). The carrier always appeared in cosine phase within its window (see Fig. 1a). In this condition, and in all other conditions, the observer's task was to determine whether the target Gabor was tilted clockwise or counter-clockwise by 8 degrees of vertical.

#### 2.2.2. Grating surround

In the surround conditions, the target was surrounded by a luminance grating. It had the same contrast and spatial frequency as the target, and a central aperture with a radius of  $0.7^\circ$ . Since the orientation and phase of surround stimuli have been found to influence performance on a number of tasks, such as contour integration (i.e. Field, Hayes, & Hess, 1993), contrast facilitation (Solo-

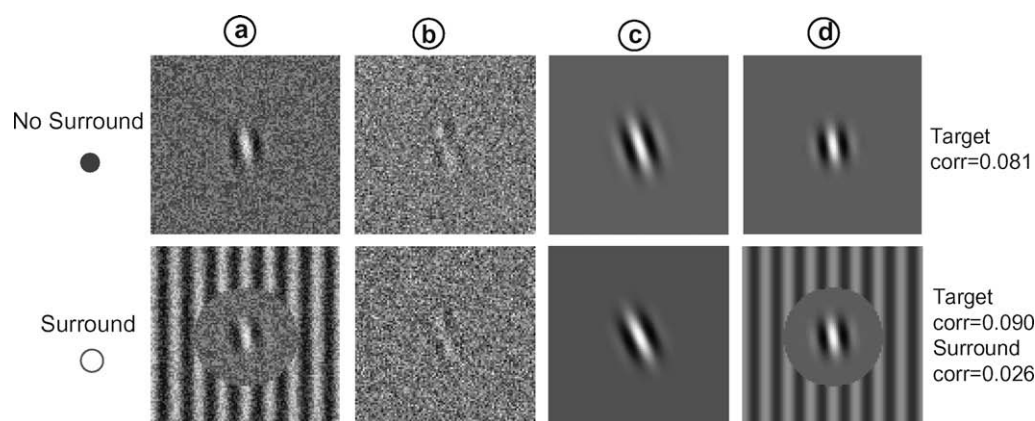
mon & Morgan, 2000; Williams & Hess, 1998) and apparent contrast (Cannon & Fullenkamp, 1991) we investigated the role of these parameters in our surround gratings. The surround gratings were either vertical or horizontal and were fully embedded within the noise. Four different surround conditions were investigated in separate blocks: target and surround approximately in phase, target and surround approximately  $180^\circ$  out of phase, target and surround approximately perpendicular, and target and surround approximately in phase with only the target contrast varying (see Fig. 2 for illustrations). In this last condition, the grating was held at 25% contrast for observers I.M. and A.T. It was held at 40% contrast for J.A.S. The order of blocks was randomised to avoid confounding the type of surround with practice and/or fatigue.

#### 2.2.3. Flanking Gabor and plaid stimuli

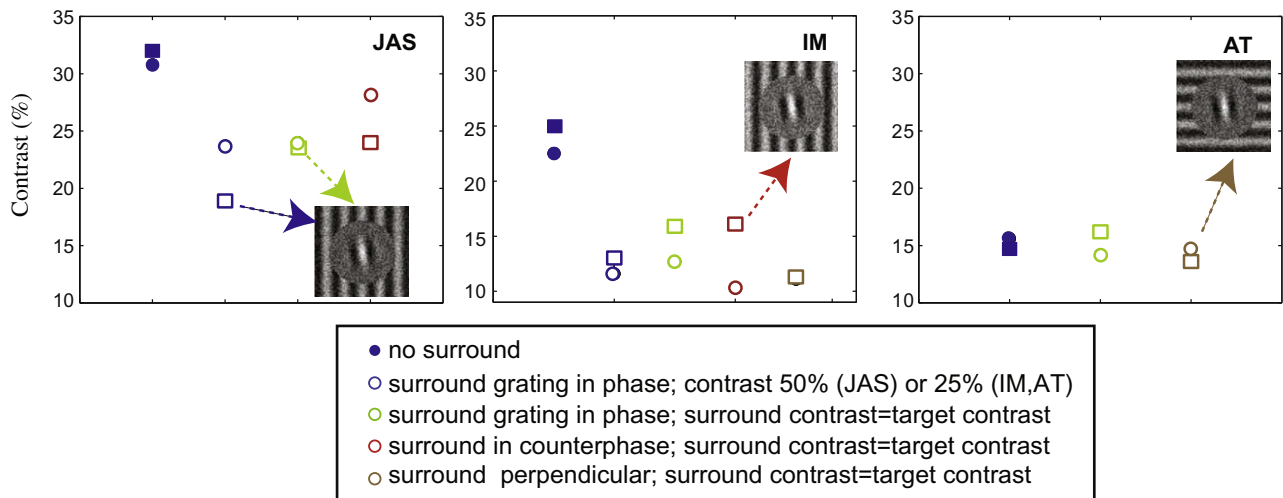
In subsequent control conditions to test for crowding using stimuli embedded in noise, two different types of visual context were used. The first was similar to that used by Parkes et al. (2001) and consisted of eight Gabors arranged in a circle around the target (see Fig. 4 for illustration). Each of these Gabors was identical to the target, except it was perfectly vertical. Center-center spacing of the target and each surround patch was  $\lambda 2.5\sqrt{2}$ . This spacing was chosen so that the patches would be clearly separate, but close enough to the target to approximate the distance of the grating surround. In the second control condition (see Fig. 5 for illustration), only the two flankers along the horizontal meridian were used. Each of these two flankers was a plaid; the sum of two Gabors that were identical to the target, except that were tilted  $\pm 22.5^\circ$  away from vertical. The center-center spacing of the target and each of these flanks was increased to  $\lambda 2.5\sqrt{2}$  to avoid masking. In this one condition, the target and flankers' spread was increased to  $\sigma = 0.28^\circ$ . The contrast of the components was half that of the target.

### 2.3. Procedure

We employed a single interval, orientation identification procedure. Observers fixated a small square ( $2 \times 2$  pixels) that was present throughout stimulus duration. The observers' task was to indicate with a key-press whether the target Gabor was tilted clockwise or counter-clockwise of vertical by  $8^\circ$ . Auditory feedback followed a response error for observers IM and AT. The contrast of the target was varied using a staircase procedure that reduced the



**Fig. 1.** Classification image technique and fitting procedure. (a) The stimulus was a Gabor oriented  $\pm 8^\circ$  of vertical presented alone (top) or with a grating surround (bottom). (b) Classification images were obtained as the sum of all noise samples leading to a correct response minus noise samples leading to an incorrect response. (c) Since the task is discrimination between two oriented targets, the optimal template is the difference between the two possible targets. Consequently, classification image data were fit with the difference of two component templates (one CCW, the other CW), the CCW component is illustrated here (see Mareschal et al. (2006) for details) and (d) Stimuli (two targets, one surround) with contrast proportional to their correlation with the classification-image shown in (b).



**Fig. 2.** Contrast thresholds measured for three observers in the left (square symbols) and right (circle symbols) visual fields. Filled symbols are thresholds obtained without a surround, open symbols are thresholds measured in the different surround conditions.

contrast by 1/3 dB or increased it by 1dB following a correct or incorrect response respectively (Kaernbach, 1991; Wetherill & Levitt, 1965). This procedure converges on the stimulus contrast (threshold) eliciting 75% correct discrimination. Observers completed 5000 (I.M.), 7000 (A.T.) or 10,000 (J.A.S.) trials in the target alone condition and 7000 (I.M., A.T.) or 10,000 (J.A.S.) trials in target and surround conditions, in blocks of 1000 (I.M., A.T.) or 500 (J.A.S.).

#### 2.4. Classification images

For a given target orientation, on any given trial, subjects could make one of two possible responses (clockwise (C) or counter-clockwise (CC) of vertical) for the two possible target configurations (stimulus clockwise (SC) or stimulus counter-clockwise (SCC) of vertical). This yields four stimulus-response combinations (denoted C-SC, C-SCC, CC-SC and CC-SCC). Noise images were summed according to whether they elicited a correct or incorrect response (clockwise noise images were flipped about the vertical axis of symmetry, so that all decision templates appear to prefer “counter-clockwise”, see Fig. 1). The difference image between the correct and incorrect response noise images gives the “correct response” classification image. In our procedure, correct and incorrect noise images were weighted equally.

#### 2.5. Parameter fitting procedure

We fit a 4-parameter decision template to the classification image from each observer in each condition. The fitting procedure has been described elsewhere (Mareschal et al., 2006) and is formed by taking the difference between one Gabor with a Counter-CW tilt and another Gabor with a CW tilt. In Mareschal et al., a weighted difference between the two Gabors was taken, where a weight  $w=1$  indicates that the decision template is a pure Gabor;  $w=0.5$  indicates an equal contribution from the two component templates, giving the decision template a checkerboard appearance. In this fitting procedure, we kept the contribution of the two components equal. The two component Gabors were constrained to have equal-but-opposite tilts, equal spatial frequencies and equal spatial spreads, but the spread along the carrier  $\sigma_1$  was allowed to differ from the spread across  $\sigma_2$ . Error bars containing the 95% confidence intervals for each parameter were derived using a bootstrapping procedure (Mareschal et al., 2006).

If performance were solely limited by stimulus noise, the most efficient decision template would be identical to the difference between the CCW and CW targets. Specifically, if we use the vector  $\mathbf{w}_i$  to denote this ideal template, then

$$\mathbf{w}_i = \arg \max_{\mathbf{w}} \left| \frac{\mathbf{E}(\langle \mathbf{w}, \mathbf{s} \rangle)}{\sqrt{\text{Var}(\langle \mathbf{w}, \mathbf{s} \rangle)}} \right|, \quad (1)$$

where  $\langle \mathbf{w}, \mathbf{s} \rangle$  denotes the inner product between template  $\mathbf{w}$  and stimulus  $\mathbf{s}$ . However, if performance were limited by a stimulus-independent perturbation of this inner product (i.e. decision noise), then the denominator would not matter, and the best template would be the one that maximized  $|\mathbf{E}(\langle \mathbf{w}, \mathbf{s} \rangle)|$ , the absolute covariance between template and stimulus.

### 3. Results

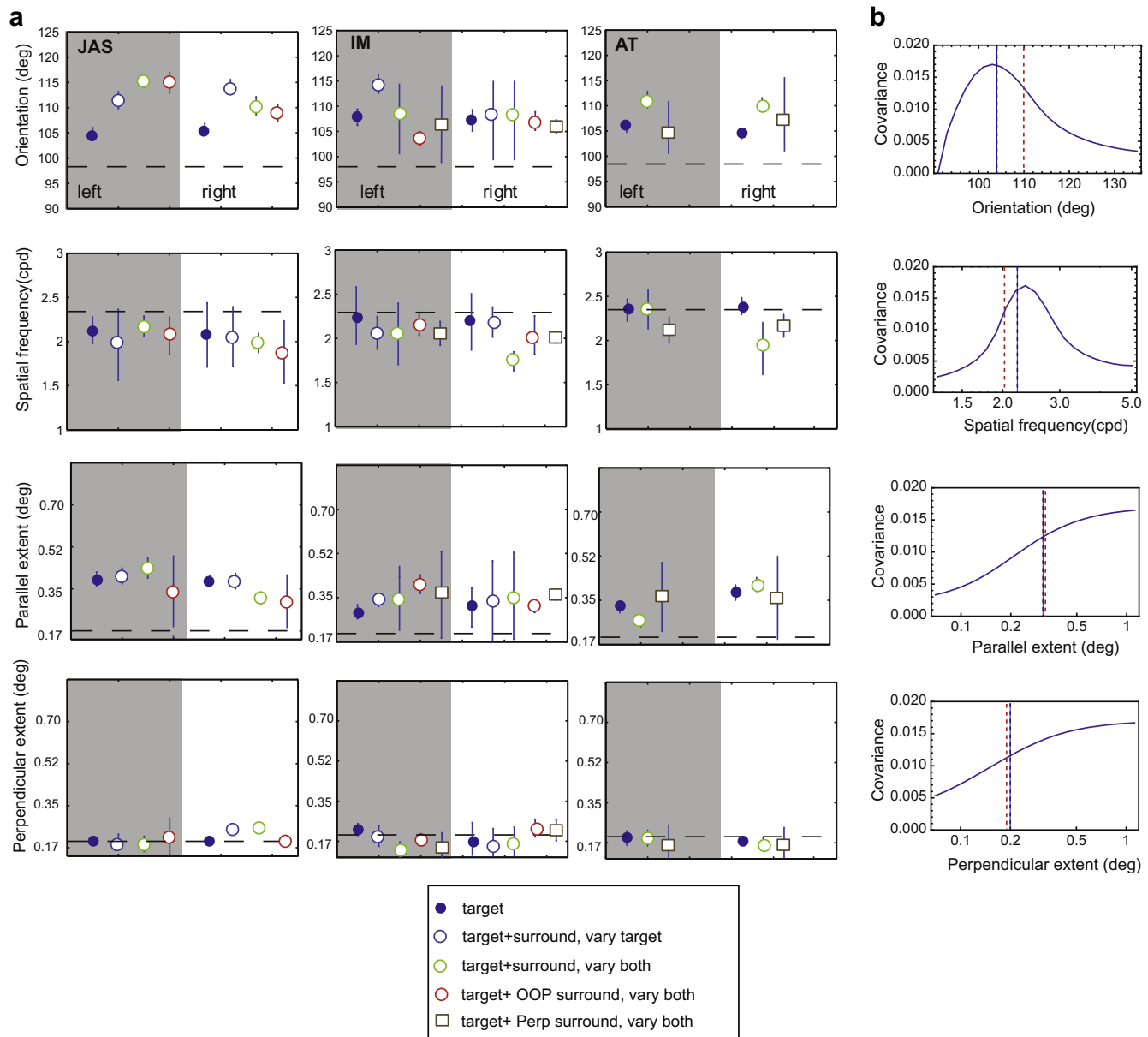
#### 3.1. Contrast thresholds

Contrast thresholds taken as the average of all reversals occurring over the last 100 trials in each run, averaged over all runs for each observer are plotted in Fig. 2. We were surprised to find that, for I.M. and J.A.S., the contrast thresholds measured without a surround (filled symbols) were higher than those measured with a surround. (The absolute thresholds for J.A.S. are higher since his noise mask was 50% contrast.) There was no effect of surround on A.T.’s threshold. This indicates that there was no crowding in the presence of our surround.

Also, thresholds measured for I.M. and J.A.S. showed differences between the left and right visual fields. For I.M., thresholds were always higher in the left visual field (square symbols), whereas the contrary was true for J.A.S. (circles) except in the target-alone condition. A.T. showed no systematic change in his thresholds. Because of these differences, the left and right visual field data were kept separate.

#### 3.2. Decision templates

In order to determine whether the changes in contrast thresholds were related to the observers using different templates to perform each task, we fit decision templates to the classification-images. Parameter values for these templates are shown in Fig. 3a. Notice that when the target was presented alone (filled



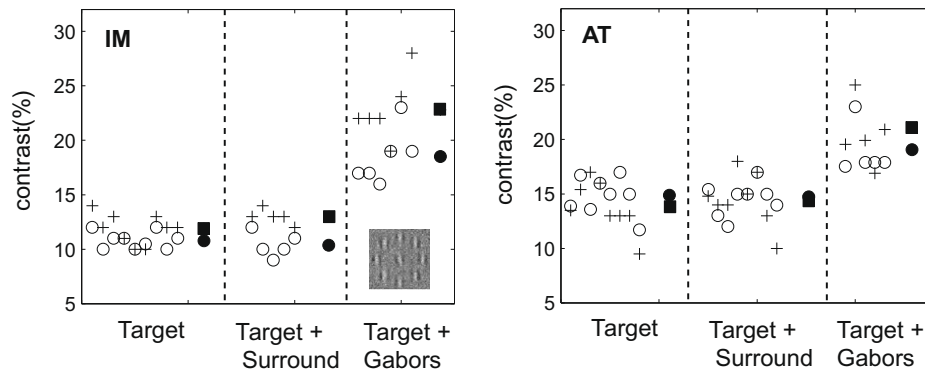
**Fig. 3.** (a) Estimates of parameters of best-fitting component templates for three observers for stimuli presented in the right visual field (white) and left visual field (grey). Dashed lines are the veridical values of the target. IM ran all conditions, JAS and AT ran a subset of the surround conditions. (b) Maximum covariance between the target and template as a function of the average value of the template parameters. Dashed red line corresponds to the average value for all surround conditions, blue for the target alone conditions (For interpretation of colour mentioned in this figure, the reader is referred to the web version of this article.).

symbols) the estimates of all template parameters were similar in both visual fields for the three subjects. This is consistent with the target-alone thresholds being relatively similar in both visual fields. Adding a surround increased the variability between the left and right visual fields, perhaps reflecting biases in observers' ability to hold fixation.

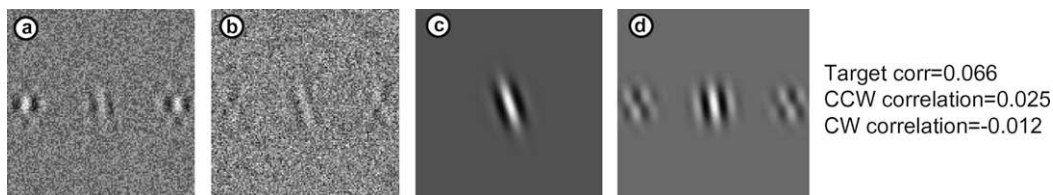
The top row plots the estimated orientation of the template. When the target was presented alone (filled symbols), the templates' orientations were more oblique than the actual target orientations. This is consistent with previous findings showing that when observers perform an orientation discrimination between two targets separated by a small orientation offset, they use the outputs of detectors tuned to orientations further away than that of the target (Mareschal et al., 2006; Solomon, 2002). In this case, the estimated orientation is approximately 5° more oblique than the actual orientation of the stimulus in either orientation.

To quantify the potential increase in covariance afforded by this "off-orientation looking," in Fig. 3b we illustrate the maximum possible covariances when each of the four parameters is fixed in turn, and the others are allowed to vary. For example, the maximum possible covariance between template and target occurs when the template's components are oriented  $\pm 13^\circ$  from vertical. This is very close to the best-fitting orientations, when averaged across all observers and both visual fields in the target alone condition (dashed blue line).

When a surround was presented with the target, the template orientation was shifted even further away from its actual orientation (and also that of the surround), particularly for vertical surrounds. Compared to the target-alone conditions, the estimated templates (averaged across all surround conditions; dashed red line) were shifted by a further 5–10°, suggesting observers use templates whose orientation is suboptimal for the task.



**Fig. 4.** Comparison of contrast thresholds with those obtained using a ring of Gabors for two observers. Filled symbols are the averages in the left (square) and right (circles) visual fields.



**Fig. 5.** Plaid crowding. (a) Stimulus, (b) classification image in the left and right visual field combined, (c) template fit to classification-image and (d), correlation between the flanker positions (tested together) and the two different components of the plaid stimulus.

The second row plots the spatial frequency of the template in the left and right visual fields. For all observers and in all conditions, the spatial frequency is lower than the actual spatial frequency of the target, possibly reflecting off frequency looking. There does not appear to be any systematic difference between the different surround and target-alone conditions (nearly all data points are within the 95% confidence intervals). Note that the maximum covariance is near the spatial frequency of the target. In the presence of a surround, observers' used templates of a slightly sub-optimal spatial frequency.

The third and fourth rows plot the vertical and horizontal extents of the template's envelope. The envelopes were larger than the target in all conditions, but only along the vertical dimension: they appeared elongated. The horizontal spread of the templates never exceeded the target dimensions. Interestingly, although it would have been beneficial to pool along the horizontal meridian to maximize covariance, observers' failed to do so. Taken together with the change in the vertical length, this supports the psychophysical finding that channels underlying observers' performance are elongated (Meese & Hess, 2007; Toet & Levi, 1992).

Finally, in order to estimate the extent (if any) to which observers incorporated the surround into their decision templates, we calculated the correlation between observers' classification-images to two types of stimuli, either the target-alone stimulus or the surround alone (Table 1).

In each condition, the correlation between classification image and target was significant ( $p < 0.05$ ) for all three observers, but it was greatest for observer I.M. Correlations between classification image and surround were significant (in three of four conditions) only for observer I.M. This can be taken as evidence that she incorporated these surrounds into her decision templates. Similar evidence from the other observers may have been obscured by greater decision noise. Alternatively, they may have actually ignored the surrounds.

### 3.3. Crowding

Initially, we formulated two hypotheses for why surrounds did not produce crowding.

- Although our targets were present on every trial and supra-threshold, it is conceivable that the surround reduced observers' spatial uncertainty by providing a cue to the location of the target.
- Parkes et al. (2001) documented strong crowding using a task similar to ours, but there were two major differences. One was the shape of the visual context. Our grating completely surrounded the target, whereas they used a ring of Gabors. The other main difference was that we added noise to the stimulus.

**Table 1**

Correlations between classification-image (left and right visual fields combined) and target, and classification-image and surround (n.s. next to correlations that were not significantly different from zero)

Stimulus		Condition				
		Target	Target + S, vary target	Target + S, vary both	Target + OOP S, vary both	Target + OOP S, vary both
		●	○	●	○	○
I.M.	Target	0.079	0.090	0.117	0.099	0.099
	Surround		0.026	−0.012 n.s.	0.031	0.021
J.A.S.	Target	0.078	0.072	0.086	0.094	
	Surround		0.007 n.s.	0.013 n.s.	−0.011 n.s.	
A.T.	Target	0.057	0.073			0.008
	Surround		0.005 n.s.			0.006 n.s.



To see if any of these factors played a role, we ran a control experiment, using a ring of Gabors, like Parkes et al., but with noise added to it.

When Parkes et al.'s (2001) ring of Gabors was used contrasts, thresholds were significantly higher in both visual fields and for both observers ( $p < 0.05$ ) than when the target was presented alone (Fig. 4). It should be noted that the target-alone thresholds for I.M. are lower than those reported in Fig. 2, though for A.T., the thresholds are the same. IM's thresholds in this experiment were measured 3 months after the initial experiment and she displayed characteristic perceptual learning. JAS was also tested on this experiment and his thresholds had similarly decreased in the target-alone condition (from 32% to 22%, both visual fields combined).

The finding here that the ring of Gabors raised thresholds rules out the role of the white noise in somehow "undoing" crowding. This is also consistent with Nandy and Tjan (2007) who measured reliable crowding using a classification image paradigm with letter stimuli. Also, it should be noted that the ring stimulus should have provided a robust spatial cue to the target's position, yet thresholds were elevated. This result is contrary to the notion that spatial uncertainty reduction was the reason for lower thresholds with the grating surround.

Best-fitting templates were similar to the ones obtained with the grating surround (IM (averaged across both visual fields): 1.85 cpd, 104.5°, 0.30° and 0.13°; A.T.: 2.28 cpd, 110°, 0.28° and 0.22°).

### 3.4. Two flankers

Crowding may occur because decision templates combine features from the flankers and the target. Alternatively observers may simply confuse flankers with the target. Either way, it should be possible to see some evidence of flankers in the classification-images. In order to increase the likelihood of this, we reduced the number of flankers to two. We attempted to maximize crowding by using plaid flankers, whose component gratings were roughly aligned with our previously estimated templates (at  $\pm 22.5^\circ$  away from vertical; see Section 2 and Fig. 5a). In a preliminary experiment, we confirmed that these flankers did significantly ( $p < 0.01$ ) raise contrast threshold from 8 to 13% for orientation discrimination ( $\pm 8^\circ$ ), but they did not affect contrast thresholds for 2AFC detection.

Classification images obtained for I.M. in the left and right visual fields were fit separately, then combined and fit again. Flanker structure is clearly visible in the combined classification-image (Fig. 5b). Best-fitting templates had a lower spatial frequency (RVF: 1.9 cpd; LVF: 1.8 cpd), but the Gaussian envelope was less elongated (RVF: 0.35°; LVF: 0.26°) than in the above experiments. Template orientations were similar (RVF: 108°; LVF: 103°). The best-fitting template to the combined (RVF + LVF) classification image is shown in Fig. 5c. This is in accord with Nandy and Tjan (2007) who reported that crowding did not affect the classification image using letter stimuli, although in their experiments they did not quantify the different classification images.

I.M. was worse when the flankers were present. Conceivably, help could have come from any noise sample that was negatively correlated with the flankers, thereby making them less visible. However, this is not what we found. Only the plaid component oppositely oriented from the target was negatively correlated ( $r = -0.012$ ) with the combined classification image. When a noise sample made the plaid component of the same orientation sign more visible, I.M. was more likely to respond correctly (see Fig. 5d). This may have been because she sometimes mistakenly used a flanker (or one component of a flanker) instead of the target to perform the task, or possibly because she used a combination of one (or both) of the flankers with the target.

We also kept the left and right visual fields separate and did not pool the different target conditions in order to test for visual field anisotropies (i.e. Bouma, 1973; Feng et al., 2007). This yielded four classification images (target CW, left visual field; target CCW left visual field; target CW, right visual field; and target CCW right visual field). Each of these was correlated with a single flanker in either the nasal or caudal position (relative to the target), but none of these correlations were significant.

## 4. Discussion

### 4.1. Configuration dependent release from crowding

Crowding occurred when the target was flanked by either two plaids or a ring of eight Gabors with vertical carriers, but not when it was wholly surrounded by a vertical grating. This finding is consistent with the growing body of literature that suggests a release from crowding for salient targets. Several studies (e.g. Felisberti, Solomon, & Morgan, 2005; Kooi, Toet, Tripathy, & Levi, 1994) have demonstrated a reduction in crowding when an irrelevant attribute (e.g. colour) is added to the flankers. By showing that performance improves with additional distractors that do not share this attribute with the target, Pöder (2006) advanced the argument that identification mechanisms are selective for generally salient stimuli, rather than those with a specific irrelevant attribute. Gheri, Morgan, and Solomon (2007) confirmed its relationship with the release from crowding, using an independent measure of target salience. The most closely related finding to ours is that of Livne and Sagi (2007), who showed that crowding was reduced or abolished when the flankers were arranged to form a continuous contour. They suggested this configuration results in defining the target as the only salient region.

### 4.2. Perceptual templates

As in all classification image analyses (e.g. Ahumada, 1996; Abbey et al., 1999; cf. Solomon, 2002), the decision templates inferred from our data make sense only within the framework of a linear classifier. The classifier's responses are determined by the computation  $\text{sgn}(\langle \mathbf{w}, \mathbf{s} \rangle + \eta)$ , where the decision noise  $\eta$  is symmetrically distributed about zero. As noted above (just after Eq (1)), the best defence against decision noise is to adopt a template whose covariance with the stimulus is high. As shown in Fig. 3b, one way to maximize covariance is to use large templates. Nonetheless, our data suggest that surrounds had virtually no effect on template size. We seem to be stuck with 0.35° along and 0.2° across.

Off-orientation looking is another way to increase the covariance between template and target (Regan & Beverley, 1985; Solomon, 2002). This explains why our observer's templates were shifted with respect to the target orientation. Without a surround, the templates were more oblique than the target by 5–10°, while the surround shifted them by a further 5–10°. However, the overall effect of this additional shift on covariance was minimal. Using the best-fitting parameter values (vertical lines in Fig. 3b), template/target covariance increased from 0.00766 to just 0.00769 when surrounds were present. This is nowhere near enough to explain why contrast thresholds were lower with a surround. Instead, the linear classifier model leaves only one option: the ratio of decision noise to template amplitude must have been lower in the presence of full grating surrounds.

It is unclear how the presence of a surround might lead to a decrease in observers' internal noise. It may be that, via a process of disinhibition, the surround inhibits vertically tuned detectors whose inhibitory influence on the CW and CCW detectors would be reduced, ultimately increasing their signal-to-noise ratios.

Although this may account for the decreased thresholds, it is unclear why this would cause templates to be further shifted in orientation.

Even in the absence of a surround, three distinct properties emerge: the templates were consistently shifted in orientation, of a lower spatial frequency and were elongated compared to the target. Off-frequency looking may be responsible for the frequency shift. The (linear) spatial frequency bandwidth of spatial frequency channels is thought to increase with frequency preference (Losada & Mullen 1995; Solomon 2000; Wilson, McFarlane, & Phillips, 1983). Since the spectrum of white noise is flat, our stimulus noise probably masked the higher frequency channels more than the lower ones. Another possibility is that the visual system shifts to lower spatial frequencies whenever stimuli are presented outside the fovea (i.e. even in the absence of noise). Consistent with this second possibility, Levi and Klein (2002) measured classification images for position discrimination in the parafovea and found that they were of a lower spatial frequency than those for position discrimination in the fovea.

The elongation of the template is consistent with several findings regarding the aspect ratio of pattern detectors (Polat & Norcia, 1998; Polat & Tyler, 1999; Toet & Levi, 1992; or see Meese & Hess, 2007 for a review). However, it should be noted that the elongation of our decision templates might reflect either the structure of a single detector or that of an integrator unit with a fixed spatial extent over which it receives inputs.

## 5. Uncited reference

(Levi et al., 2002).

## References

- Abbey, C. K., & Eckstein, M. P. (2002). Classification image analysis: estimation and statistical inference for two-alternative forced-choice experiments. *J. Vision*, 2, 66–78.
- Abbey, C. K., Eckstein, M. P., & Bochud, F. O. (1999). Estimation of human-observer templates in two-alternative forced-choice experiments. *Proc SPIE*, 2662, 284–295.
- Ahumada, A. J. (1996). Perceptual classification images from vernier acuity masked by noise. *Perception*, 25.
- Ahumada, A. J. (2002). Classification image weights and internal noise level estimation. *J. Vision*, 2, 121–131.
- Bouma, H. (1970). Interaction effects in parafoveal letter recognition. *Nature*, 116, 177–178.
- Bouma, H. (1973). Visual interference in parafoveal recognition of initial and final letters of words. *Vision Research*, 13, 767–782.
- Cannon, M. W., & Fullenkamp, S. C. (1991). Spatial interactions in apparent contrast: inhibitory effects among grating patterns of different spatial frequencies, spatial positions and orientations. *Vision Research*, 31, 1985–1998.
- Chung, S. T., Levi, D. M., & Legge, G. E. (2001). Spatial-frequency and contrast properties of crowding. *Vision Research*, 41, 1833–1850.
- Dakin, S. C., & Bex, P. J. (2003). Natural image statistics mediate brightness filling in. *Proceedings of Royal Society*, 270, 2341–2348.
- DeAngelis, G. C., Ohzawa, I., & Freeman, R. D. (1993). *Journal of Neurophysiology*, 69, 1118–1135.
- Emerson, R. C., Bergen, J. R., & Adelson, E. H. (1992). Directionally selective complex cells and the computation of motion energy in cat visual cortex. *Vision Research*, 32, 203–218.
- Felisberti, F. M., Solomon, J. A., & Morgan, M. J. (2005). The role of target salience in crowding. *Perception*, 34, 823–833.
- Feng, C., Jiang, Y., & He, S. (2007). Horizontal and vertical asymmetry in visual spatial crowding effects. *Journal of Vision*, 7(2), 1–10. 13.
- Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: evidence for a local association field. *Vision Research*, 33, 173–193.
- Gheri, C., Morgan, M. J., & Solomon, J. A. (2007). The relationship between search efficiency and crowding. *Perception*, 36, 1779–1787.
- Gold, J. M., Murray, R. F., Bennett, P. J., & Sekuler, A. B. (2000). Deriving behavioural receptive fields for visually completed contours. *Current Biology*, 10, 663–666.
- He, S., Cavanaugh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, 383, 334–337.
- Kaernbach, C. (1991). Simple adaptive testing with the weighted up-down method. *Perception & Psychophysics*, 49, 227–229.
- Kooi, F. L., Toet, A., Tripathy, S. P., & Levi, D. M. (1994). The effect of similarity and duration on spatial interaction in peripheral vision. *Spatial Vision*, 8, 255–279.
- Levi, D. M., & Klein, S. A. (2002). Classification images for detection and position discrimination in the fovea and parafovea. *Journal of Vision*, 2, 46–65.
- Levi, D. M., Klein, S. A., & Hariharan, S. (2002). Suppressive and facilitatory spatial interactions in foveal vision: Foveal crowding is simple contrast masking. *Journal of Vision*, 2, 140–166.
- Levi, D. M., Klein, S. A., & Hariharan, S. (2002). Suppressive and facilitatory spatial interactions in peripheral vision: Peripheral crowding is neither size invariant or simple contrast masking. *Journal of Vision*, 2, 167–177.
- Livne, T., & Sagi, D. (2007). Configuration influence on crowding. *Journal of Vision*, 7(2), 1–12. 4.
- Loomis, J. K. (1978). Lateral masking in foveal and eccentric vision. *Vision Research*, 18, 335–338.
- Losada, M. A., & Mullen, K. T. (1995). Color luminance spatial tuning estimated by noise masking in the absence of off-frequency looking. *Journal of the Optical Society of America*, 12, 250–260.
- Mareschal, I., Dakin, S. C., & Bex, P. J. (2006). Dynamic properties of orientation discrimination assessed using classification images. *PNAS*, 103, 5131–5136.
- Meese, T., & Hess, R. F. (2007). Anisotropy for spatial summation of elongated patches of grating: a tale of two tails. *Vision Research*, 47, 1880–1892.
- Murray, R. F., Bennett, P. J., & Sekuler, A. B. (2002). Optimal methods for calculating classification images: weighted sums. *Journal of Vision*, 2, 79–104.
- Nandy, A. S., & Tjan, B. S. (2007). The nature of letter crowding as revealed by first- and second-order classification images. *Journal of Vision*, 7, 1–26.
- Neri, P., & Heeger, D. J. (2002). Spatiotemporal mechanisms for detecting and identifying image features in human vision. *Nature Neuroscience*, 8, 812–816.
- Ohzawa, I., DeAngelis, G. C., & Freeman, R. D. (1997). Encoding of binocular disparity by complex cells in the cat's visual cortex. *Journal of Neurophysiology*, 77, 2879–2909.
- Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging or crowded orientation signals in human vision. *Nature Neuroscience*, 4, 739–744.
- Pelli, D. G., Palomares, M., & Majaj, N. J. (2004). Crowding is unlike ordinary masking: distinguishing feature integration from detection. *Journal of Vision*, 4, 1136–1169.
- Petrov, Y., Popple, A. V., & Mc Kee, S. (2007). Crowding and surround suppression: not to be confused. *Journal of Vision*, 7, 1–9.
- Poder, E. (2006). Crowding, feature integration and two kinds of attention. *Journal of Vision*, 6, 163–169.
- Polat, U., & Norcia, A. M. (1998). Elongated physiological summation pools in the human visual cortex. *Vision Research*, 38, 3735–3741.
- Polat, U., & Tyler, C. W. (1999). What pattern the eye sees best. *Vision Research*, 39, 887–895.
- Regan, D., & Beverley, K. I. (1985). Postadaptation orientation discrimination. *Journal of the Optical Society of America*, 2, 147–155.
- Ringach, D. L., Hawken, M. J., & Shapley, R. (1997). Dynamics of orientation tuning in macaque primary visual cortex. *Nature*, 387, 281–284.
- Solomon, J. A. (2000). Channel selection with non-white-noise masks. *Journal of the Optical Society of America*, 17, 986–993.
- Solomon, J. A., & Morgan, M. J. (2000). Facilitation from collinear flanks is canceled by non-collinear flanks. *Vision Research*, 40, 279–286.
- Solomon, J. A. (2002). Noise reveals visual mechanisms of detection and discrimination. *Journal of Vision*, 2, 105–120.
- Strasburger, H. (2005). Unfocused spatial attention underlies the crowding effect in indirect form vision. *Journal of Vision*, 5, 1024–1037.
- Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision Research*, 32, 1349–1357.
- Tripathy, S. P., & Cavanaugh, P. (2002). The extent of crowding in peripheral vision does not scale with target size. *Vision Research*, 42, 2357–2369.
- Wetherill, G. B., & Levitt, H. (1965). Sequential estimation of points on a psychometric function. *Mathematical and Statistical Psychology*, 18, 1–10.
- Wilkinson, F., Wilson, H. R., & Ellember, D. (1997). Lateral interactions in peripherally viewed texture arrays. *Journal of the Optical Society of America*, 14, 2057–2068.
- Williams, C. B., & Hess, R. F. (1998). Relationship between facilitation at threshold and suprathreshold contour integration. *Journal of the Optical Society of America*, 15, 2046–2051.
- Wilson, H. R., McFarlane, D. K., & Phillips, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Vision Research*, 23, 873–882.